

# Structure and dynamics of food webs in Andean lakes

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## Abstract

Food webs from oligotrophic Andean lakes of Bariloche region (41°S) are described. Their peculiarities in comparison with Northern Hemisphere studies are noted. The endemic species composition, the extended euphotic zone, and the oxygenated bottom allow a particular structure of the pelagic and benthic food webs. Experimental work with pelagic communities indicates that models based only on zooplankton body size are questionable and that nutrient enrichment does not necessarily lead to a positive effect on herbivorous populations. Invertebrate predation effects depend on the lake and type of predator, while vertebrate predation does control crustacean populations. The characteristic low species richness of top predators is likely to change following the introduction of exotic salmonids. The benthic food web is quite distinctive with a slow rate of decaying organic matter and easily altered by the introduction of exotic tree species.

## Key words

benthos, food web interactions, plankton, South Andes lakes

## INTRODUCTION

Water quality reflects external impacts on the ecosystem and their transformation through biotic interactions within the aquatic ecosystem. Although nutrients determine the biotic response of lakes, the final result has a strong dependence on the structure of the biotic community (Shapiro 1980). Thus, lake ecosystems are complex, and much of the unexplained variance in lake productivity under similar nutrient concentration is due to differences in food web dynamics (Carpenter 1987).

North Andean Patagonian oligotrophic lakes have some peculiarities in the food web structure which influence ecosystem dynamics. In this contribution, we note these features as a tool for, or a consequence of lake management. Deliberate or accidental introduction of species, as well as other practices, are likely to change trophic web structure, and thus produce unexpected effects on the whole lake.

## STUDY AREA

The study was carried out on lakes at 41°S on the east side of the Andes (Fig. 1). The area is included in the Nahuel

Huapi National Park which has an important hydrographic system including many glacial lakes and low order streams and rivers. The climate is classified as temperate cool, with fall and winter precipitation ranging from 2700 to 500 mm y<sup>-1</sup>. The lake district has been named by Thomasson (1963) as Araucanian Lakes (east of the Andes), and comprises a large number of lakes including large and deep ones (surface >5 km<sup>2</sup>, depth >100 m) and small and shallow ones (surface <5 km<sup>2</sup>, depth <12 m) (Fig. 1). The waters are very dilute and dominated by calcium, bicarbonate and dissolved silica (Pedrozo *et al.* 1993). The lakes range from ultraoligotrophic to oligotrophic and most are warm monomictic. Nevertheless, small lakes are dimictic or cold polymictic, depending on depth. A great number of these lakes has been successfully colonized by salmonids (Quirós 1997) introduced early this century.

The vegetation of the area is mainly composed of evergreen and deciduous *Nothofagus* forest. In particular, low order streams are covered by the deciduous tree locally named 'lenga' (*Nothofagus pumilio* (P. et E.) Krasser).

## METHODS

Information on food webs in Andean lakes comes from several sources, including papers on general limnology (Pedrozo *et al.* 1993; Morris *et al.* 1995), plankton structure and succession (Balseiro & Modenutti 1990; Díaz & Pedrozo 1993; Modenutti 1993, 1997; Queimaliños 1997), and early

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fish life history (Cussac *et al.* 1992). Data on the differential effects of linkage between trophic levels come mainly from

our own experimental work (Table 1). The whole set includes laboratory and field experiments. Field manipulative experiments were carried out in small (<1 km<sup>2</sup>) and shallow (<12 m) lakes. However, benthonic food web studies were performed in low order streams of the same area.

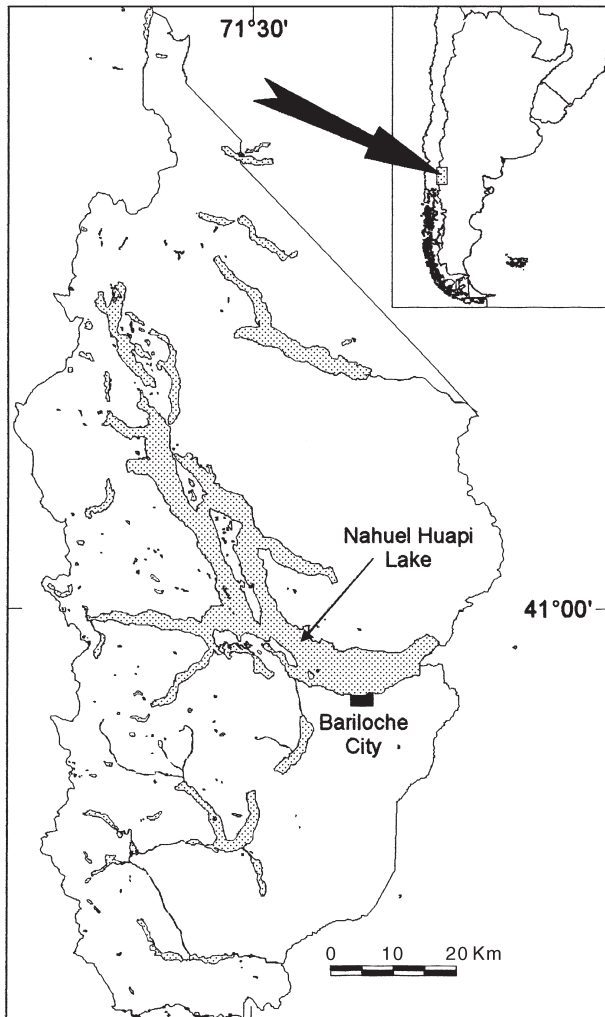


Fig. 1. Map of the Nahuel Huapi National Park, Argentina.

## RESULTS AND DISCUSSION

### Pelagic food web

Plankton assemblages in lakes located in the Bariloche region (41°S) have a simple structure. Phytoplankton is dominated by nanoplanktonic flagellated cells such as the chrysophycean *Chrysochromulina parva* Lackey and the cryptophycean *Rhodomonas lacustris* (Pascher & Ruttner) Javornicky. This fraction plays an important role in the trophic food web because it constitutes the main food for zooplankton. Moreover, there is an absence of blue-green blooms and the net phytoplankton is dominated by diatoms like *Asterionella formosa* Hassall and *Aulacoseira granulata* (Ehr.) Simonsen, large chrysophyceans (*Dinobryon* spp.) and dinoflagellates (*Gymnodinium* spp. and *Peridinium* spp.). Zooplankton is characterized by the dominance of rotifers and small crustaceans (<1 mm body length). Cladocerans are represented by species of *Bosmina* (*B. longirostris* (O.F.M.) as dominant and *B. chilensis* Daday in lower proportions) and *Ceriodaphnia dubia* Richard. Copepods are mainly calanoids of the genus *Boeckella*. *Boeckella gracilipes* Daday has a widespread distribution among the lakes and is dominant in the pelagic zone, while *B. gibbosa* (Brehm) and *B. brevicaudata* (Brady) have a restricted distribution in temporary ponds or fishless lakes. Cyclopoid copepods are quite under-represented numerically.

Protozoan plankton is dominated by large ciliates (>100 µm) such as *Stentor araucanus* Foissner & Wölf and *Ophrydium naumanni* Pejler. These species are restricted

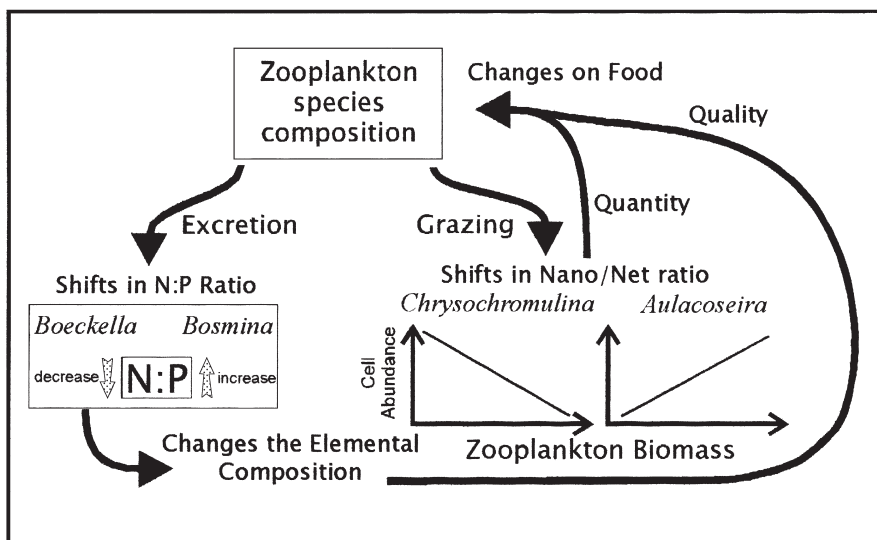


Fig. 2. Direct and indirect interactions between grazers, phytoplankton, and nutrients in the pelagic food web. The decrease or increase in N:P ratio is based on Balseiro *et al.* (1997). The graphs within the figure indicate the opposite responses of cell abundance to grazing effect, based on own field experiments.

to large lakes (>5 km<sup>2</sup>), where they develop important populations within the extended euphotic zone (40–50 m) (Modenutti 1997). This particular vertical and spatial distribution is due to the resistance of these organisms to high irradiation (Modenutti *et al.* 1997), which is characteristic of the upper levels of the large oligotrophic lakes with low dissolved organic carbon concentrations (Morris *et al.* 1995). These large ciliates have stable associations with symbiotic green algae (*Chlorella*), reaching up to 2000 cells per ciliate (Modenutti 1988; Foissner & Wölf 1994). Thus, con-

siderations concerning chlorophyll *a* concentrations must be taken seriously.

The main cladoceran species feed on nanoplankton and have a high niche overlap. For *B. longirostris* and *C. dubia*, this overlap, estimated through the Pianka index, ranged from 0.874 to 0.929, corresponding to different phytoplankton conditions (Matveev & Balseiro 1990). Thus, competition may play an important role in the regulation of zooplankton populations. With nutrient enrichment, phytoplankton composition changed to a codominance of the

**Table 1.** Summary of scientific publications concerning experiments on trophic relationships in lakes of the Bariloche region

Waterbody	Period	Type	Process	Duration	Variable	References
Laguna Ezquerra	March–April 1988	<i>In vitro</i>	Cladocerans and food quality	45 days	Fecundity	Matveev & Balseiro 1990
Laguna Ezquerra	March 1991 February–March 1992	<i>In situ</i> (Enclosures 250 L)	Small zooplankton–phytoplankton interaction	6–15 days	Phytoplankton species composition	Queimaliños 1993; Queimaliños & Modenutti 1993
Laguna Ezquerra	October 1988– March 1989	<i>In vitro</i>	Cladocerans and food resources	6 months	Fecundity	Balseiro <i>et al.</i> 1992
Laguna Ezquerra	October 1988– March 1990	<i>In vitro</i>	Water mites predation	24 h each	Predation rates	Balseiro 1992; Diéguez <i>et al.</i> 1997
Laguna Ezquerra	February 1988– November 1992	<i>In vitro</i>	Feeding experiments with small cladocerans	20 h each	Feeding rates–niche overlap	Matveev & Balseiro 1990; Queimaliños 1993
Laguna Fantasma	August–December 1989 September–December 1992 May–December 1994	<i>In vitro</i>	<i>Parabroteas sarsi</i> predation on cladocerans and rotifers	24 h each	Predation rates	Balseiro & Vega 1994; Vega 1995; Diéguez & Balseiro 1997
Lake Gutiérrez	November 1994– February 1995	<i>In vitro</i> and <i>in situ</i>	<i>Stentor araucanus</i> culture	48–72 h and 3 days	Mortality	Modenutti <i>et al.</i> 1998
Lake El Trébol	November 1995– February 1996	<i>In situ</i> (2 L bottles)	Nutrient recycling	72 h each	Zooplankton biomass– nutrient concentration	Balseiro <i>et al.</i> 1997
Lake El Trébol	November 1995– February 1996	<i>In situ</i> (2 L bottles)	Phytoplankton–zooplankton interactions	72 h each	Phytoplankton density and species composition	Queimaliños <i>et al.</i> 1998
Lake Moreno	November 1995– February 1996	<i>In situ</i> (2 L bottles)	Nutrient recycling	5 days	Zooplankton biomass– TP and TDP concentrations—Chl <i>a</i>	E. Balseiro, unpubl. data, 1996
Ñireco stream	May–September 1995 November 1995– March 1996	<i>In situ</i> (leave litter bags)	Processing of organic matter by macroinvertebrates	4–5 months	Weight loss of CPOM	Albariño 1996, 1997b
Ñireco stream	February 1996	<i>In vitro</i>	Feeding behaviour of shredders	21 days	Feeding signals on leaves (CPOM)	Albariño & Valverde 1998

cyanobacteria *Chroococcus minor* (Kütz.) Nag. and flagellated cells. We observed that this new phytoplankton composition led to a drastic decrease in *Ceriodaphnia* fecundity but not in *Bosmina*. These results imply that the nutritional value of a particular species of algae for a given zooplankton species is important in determining the outcome of competition in these lakes. Moreover, the nutrient enrichment of lake water does not necessarily lead to a positive effect on herbivorous populations (Matveev & Balseiro 1990).

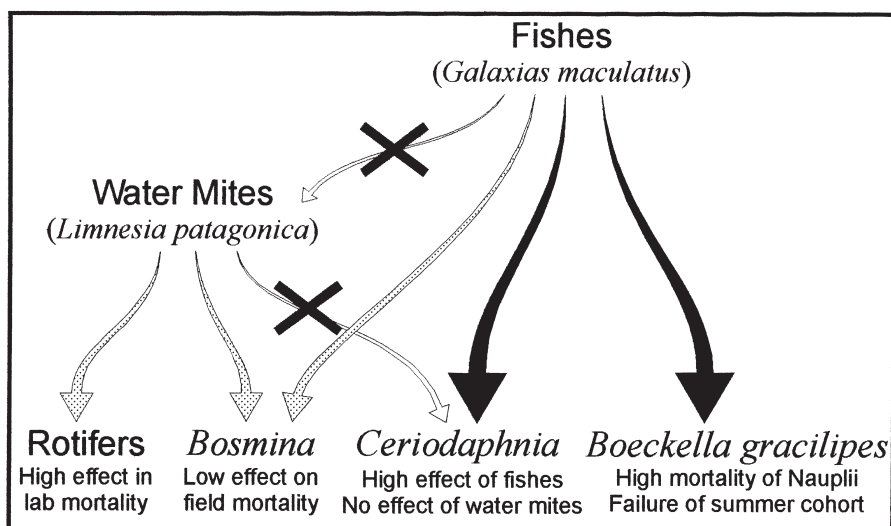
The particular effect of small-sized zooplankton on the phytoplankton is of primary interest, since in Northern Hemisphere models zooplankton communities differ sharply in body size. Herbivorous zooplankton have two contrasting effects on phytoplankton. On the one hand, grazing decreases nanoplankton abundance and, as a result, changes the nano-net phytoplankton ratio (Fig. 2). On the other hand, zooplankton excretion may shift the nutrient supply ratio for algae and, therefore, provoke changes in element limitation and food quality for zooplankton (Fig. 2). On this basis, we performed field incubation experiments with increased zooplankton biomass (Balseiro *et al.* 1997). Cladocerans and copepods release phosphorus and nitrogen mainly as dis-

solved compounds (Peters 1975; Lehman 1984), and these dissolved fractions of nitrogen (N) and phosphorus (P) are available for algal uptake. These herbivorous crustaceans possess a rather rigid stoichiometry but different species may differ greatly (Andersen & Hessen 1991). Consequently, they release nutrients in different ratios according to the species involved. In southern Andes lakes, zooplankton succession is characterized by a change in the dominance from the calanoid copepod *Boeckella gracilipes* in winter and spring, to the cladoceran *Bosmina longirostris* in mid-summer, and the rotifer *Polyarthra vulgaris* Carlin in late summer (Balseiro & Modenutti 1990; Balseiro *et al.* 1992; Modenutti 1994). Through field incubation experiments, we observed that these changes in zooplankton composition over the annual cycle alter the nutrient supply ratio. *Boeckella gracilipes* lowers the N:P ratio decreasing the P limitation, whereas *Bosmina longirostris* tends to increase this ratio and therefore increase the P limitation during summer (Balseiro *et al.* 1997). This situation clearly shows the interdependence between zooplankton nutrient recycling and community species composition (Fig. 2).

The grazing effect of these small herbivores produces a differential impact on phytoplankton <20  $\mu\text{m}$  Greatest Axial Linear Dimension (GALD). Through enclosure experiments with *Polyarthra* and *Bosmina* as dominant zooplankters, opposite responses of the phytoplankton fraction <5  $\mu\text{m}$  were observed. However, the fraction >20  $\mu\text{m}$  did not change significantly (Queimaliños & Modenutti 1993). Further field experiments carried out with a different zooplankton composition and biomass indicate that the development of the diatom *Aulacoseira granulata* results from heavy grazing on nanoflagellates, such as *Chrysochromulina parva*. Then, the nutrients recycled by zooplankton are of benefit to the net phytoplankton algae (Queimaliños *et al.*

**Table 2.** Main invertebrate predator features in Andean lakes

Predator	Predator size	Prey	Distribution
<i>Limnesia patagonica</i>	1.5 mm	Rotifers	Widespread
Lundbald		Cladocerans	
<i>Boeckella gibbosa</i> (Brehm)	1.15 mm	Rotifers	High mountain fishless lakes
<i>Parabroteas sarsii</i> Daday	4.5 mm	Rotifers	Temporary pools, fishless lakes
		Cladocerans	
		Copepods	



**Fig. 3.** Relationships between intermediate and upper levels in the Laguna Ezquerria (Río Negro, Argentina) pelagic food web. X, absence of interaction; grey arrows, low effect; black arrows, strong effect.

1998). We observed opposite responses between zooplankton biomass and cell abundance of the nanoplanktonic *C. parva* and the netphytoplankton *A. granulata* (Fig. 2). These results outline the importance of grazing as a growth limiting factor for *C. parva* abundance, and the indirect effect of zooplankton, through nutrient recycling, in the development of diatoms.

The importance of different invertebrate predators in controlling and structuring zooplankton communities is still the subject of controversy. Besides, the invertebrate predators present in North Patagonian Andean lakes are unknown or little known in Northern Hemisphere lakes. In Andean lakes, the absence of *Chaoborus* and *Leptodora* is noteworthy, while a water-mite and two calanoid copepods are the most important invertebrate predators (Table 2). Nevertheless, these organisms are not widespread since their presence is restricted to particular lakes. Through laboratory experiments, we determined that the water-mite *Limnesia patagonica* Lundbald can effectively impact rotifers and the cladoceran *B. longirostris* but not *C. dubia* (Balseiro 1992; Diéguez *et al.* 1997) (Fig. 3). However, the contribution of *Limnesia* to *Bosmina*'s mortality in the field is too low to provoke prey suppression because of the low density of the predator (Balseiro 1992). This limited effect is shown in Fig. 3 by the grey arrow. Since *Limnesia* is not eaten by fishes, the observed low density in nature cannot be attributed to predation (Fig. 3).

The predaceous calanoid *Parabroteas sarsi* (Daday) consumes a great variety of prey including rotifers, cladocerans and copepods (Balseiro & Vega 1994; Vega 1995), while *Boeckella gibbosa* eats rotifers at the end of its development (Modenutti 1993). However, the distribution of these predators is restricted to temporary or fishless ponds (Table 2).

Autochthonous fish fauna in lakes of the Bariloche region is essentially poor in species number compared with tropical and subtropical fauna. There are very few piscivorous fishes; only the native Patagonian perch (*Percichthys colhuapiensis* McDonagh) has been reported as piscivorous in adult stages. However, this scenario has been modified by the introduction of exotic salmonids, in particular species of *Salmo* and *Salvelinus*, which are often considered as piscivorous (Quirós 1998). Planktivory is mainly exerted by fish larvae and juveniles of Galaxiidae and Atherinidae (Cervellini *et al.* 1993; Modenutti *et al.* 1993). Larvae prefer copepod nauplii, while juveniles feed on cladocerans. In particular, larvae and juveniles of *Galaxias maculatus* Jennyns can affect the populations of the copepod *B. gracilipes* by preying on nauplii. This predation causes the failure of the summer cohort of *B. gracilipes*, and also prevents the reappearance of the cladoceran *Ceriodaphnia dubia* in the mid-summer plankton (Fig. 3) (Modenutti *et al.* 1993).

## Benthonic food web

Benthic primary producers include macrophytes and periphyton. The former are restricted to particular areas where the wind motion and the profile of the lake allow the colonization. However, the presence of Characeae (*Nitella* sp.) in the illuminated bottom of the lakes is very common. Periphyton communities are dominated by diatoms and develop on the surface of a great variety of substrates. Herbivory is important in the regulation of periphyton, and the intensity of control depends on the type of herbivores involved (Gaglioti 1993).

Zoobenthos is highly diverse with many endemic species. The littoral offers many habitats and thus increased species richness and abundance when compared with the profundal zone (Añón Suárez 1991). As the lakes are oligotrophic, the profundal zoobenthos is diverse and requires oxygen. Within the Chironomidae, tanypodines, orthocladines and species of the genus *Tanytarsus* are the main components. The food web in the profundal is based on detritivorous and carnivorous midges, with low values of secondary production (Añón Suárez 1997).

## Watershed management

Since streams are considered as heterotrophic functioning systems, the cycling or spiralling of organic matter represents a crucial functional aspect of these water-bodies. Streams are thus dependent on the watershed in terms of movement of organic matter. Therefore, impacts on the basin

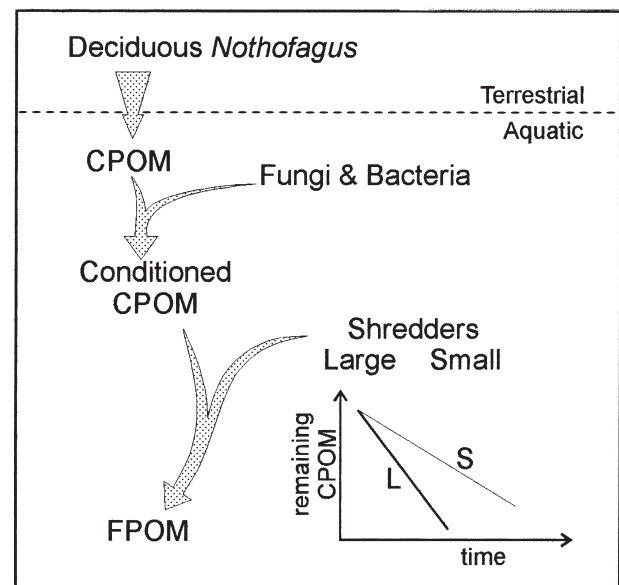


Fig. 4. Relationships between CPOM and shredders in a low order stream of South Andes. The graph within the figure indicates different decaying rates for large (L) and small (S) shredders, based on own data.



**Table 3.** Comparison of the decaying rates obtained from South Andes and Northern Hemisphere low order streams

Leaf species	Locality	T <sub>50</sub>	Temperature		References
			(°C)	k	
<i>Quercus alba</i>	Michigan, USA		5	0.0049	Rowe <i>et al.</i> 1996
<i>Salix lucida</i>	Michigan, USA	46	3–4		Petersen & Cummins 1974
<i>Populus tremuloides</i>	Colorado, USA		0	0.0077	Short <i>et al.</i> 1980
<i>Pinus ponderosa</i>	Colorado, USA		0	0.0038	Short <i>et al.</i> 1980
<i>Pseudotsuga menziesii</i>	Oregon, USA	89	8		Sedell <i>et al.</i> 1974
<i>Nothofagus solandri</i> var. <i>cliffortioides</i>	New Zealand	152	5.5–14		Davis & Winterbourn 1977
<i>Nothofagus fusca</i>	New Zealand	37	6–14		Linklater 1995
<i>Nothofagus pumilio</i> smaller shredders	South Andes, Argentina	122	9	0.0057	Albariño 1997b
<i>Nothofagus pumilio</i> large shredders	South Andes, Argentina	89	9	0.0078	Albariño 1997b
<i>Nothofagus pumilio</i>	South Andes, Argentina	216	0–5	0.0032	Albariño 1996
<i>Pinus ponderosa</i>	South Andes, Argentina	407	0–5	0.0017	Albariño 1996

(e.g. deforestation) can cause dramatic effects on streams and, consequently, in lakes which receive those altered tributaries. In the North Andean Patagonian region, the vegetation of the main basins correspond to *Nothofagus* forest, and so streams are heavily shaded and receive leaf litter from these autochthonous trees. The main benthic shredders that process this organic matter are endemic species of Plecopteran, Trichopteran and Dipteran larvae (Albariño 1997a; Valverde & Albariño 1997). We observed that the processing rates of leaf litter are highly dependent on shredder size (Fig. 4, Table 3). The introduction of exotic fishes or the enhancement of fish populations may shift the shredder population size structure towards smaller forms. As a consequence, the decaying rates of leaf litter may be significantly lower (Table 3).

Experimental studies have shown that the decaying rates of *N. pumilio* (lenga) due to shredders are naturally slow in comparison with those of other tree species of temperate areas of the world (Albariño 1997b) (Table 3). Thus, benthic food webs have slow processing rates of organic matter and can easily be altered by the introduction of exotic tree species. In a low order Andean stream, Albariño (1996) determined that the decaying rates of exotic *Pinus* needles are much lower than those calculated for the leaves of the autochthonous *N. pumilio*. Moreover, *Pinus* needles showed slower decaying rates in South Andes than those measured in the Northern Hemisphere (Table 3). These results support the idea that the introduction of exotic species of *Pinus* modifies the quantity and quality of the organic matter that enters the lakes.

## Perspectives

In lakes of the Andean region, pelagic food webs show peculiarities due to the scarcity of top predators, as well as the structure of intermediate and lower levels of the food chain. Manipulative experiments carried out in these lakes (Table 1) indicate that contrasting responses would be expected. Any manipulation such as nutrient enrichment, species translocation or the introduction of exotic species will affect the ecosystem through alterations at different levels of the food web. The extrapolation of Northern Hemisphere results is unlikely to be valid due to the complexity of responses at intermediate and low levels. Therefore, it is essential to focus attention on all levels because the consequences of lake management depend greatly on the particular food web structure and level affected. Practical experimentation appears to be a central tool for the research and management of these ecosystems.

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## REFERENCES

- Albariño R. J. (1996) Dinámica del procesamiento de la materia orgánica particulada gruesa por el macrozoobentos en arroyos andinos. *II Taller de Bentos*, Santa Fe: 1.
- Albariño R. J. (1997a) Spatial distribution of Plecoptera from an Andean-Patagonian Lotic Environment in Argentina. *Rev. Brasil. Biol.* **57**, 629–636.

- Albariño R. J. (1997b) Colonisation and processing rates of *Nothofagus pumilio* leaves by macroinvertebrates in a Patagonian mountain stream (Argentina). *Noticiario de Biología* **5**, 133.
- Albariño R. J. & Valverde A. C. (1998) Hábito alimentario del estado larval de *Parasericostoma cristatum* (Trichoptera: Sericostomatidae). *Rev. Soc. Entomol. Argent.* **57**, 131–135.
- Andersen T. & Hessen D. O. (1991) Carbon, nitrogen, and phosphorus content of freshwater zooplankton. *Limnol. Oceanogr.* **36**, 807–814.
- Añón Suárez D. (1991) Distribución del bentos del lago Escondido (Río Negro, Argentina) con especial énfasis en los quironómidos (Diptera, Chironomidae). *Stud. Neotrop. Fauna Environ.* **26**, 149–157.
- Añón Suárez D. (1997) Estructura y dinámica de la taxocenosis Chironomidae (Diptera, Nematocera) de un lago Andino. Tesis Doctoral. Fac.Cs.Nat y Museo. UNLP (in Spanish).
- Balseiro E. G. (1992) The role of pelagic watermites in the control of cladoceran population in a temperate lake of the Southern Andes. *J. Plankton Res.* **14**, 1267–1277.
- Balseiro E. G. & Modenutti B. E. (1990) Zooplankton Dynamics of Lake Escondido (Río Negro, Argentina) with special reference to a population of *Boeckella gracilipes* (Copepoda, Calanoida). *Int. Rev. gesam. Hydrobiol.* **75**, 475–491.
- Balseiro E. G. & Vega M. (1994) Vulnerability of *Daphnia middendorffiana* to *Parabroteas sarsi* predation: the role of the tail spine. *J. Plankton Res.* **19**, 783–793.
- Balseiro E. G., Modenutti B. E. & Queimaliños C. P. (1992) The coexistence of *Bosmina* and *Ceriodaphnia* in a South Andes lake: an analysis of demographic responses. *Freshwat. Biol.* **28**, 93–101.
- Balseiro E. G., Modenutti B. E. & Queimaliños C. P. (1997) Nutrient recycling and shifts in N:P ratio by different zooplankton structures in a South Andes lake. *J. Plankton Res.* **19**, 805–817.
- Carpenter S. R. (1987) *Complex Interactions in Lake Communities*. Springer Verlag, New York.
- Cervellini P. V., Battini M. & Cussac V. (1993) Ontogenetic shifts in the diet of *Galaxias maculatus* (Galaxiidae) and *Odontesthes microlepidotus* (Atherinidae). *Environ. Biol. Fishes* **36**, 283–290.
- Cussac V., Cervellini P. V. & Battini M. (1992) Intralacustrine movements of *Galaxias maculatus* (Galaxiidae) and *Odontesthes microlepidotus* (Atherinidae) during their early life history. *Environ. Biol. Fishes* **35**, 141–148.
- Davis S. F. & Winterbourn M. J. (1977) Breakdown and colonization of *Nothofagus* leaves in a New Zealand stream. *Oikos* **28**, 250–255.
- Diaz M. M. & Pedrozo F. (1993) Seasonal succession of phytoplankton in a small Andean Patagonian lake (Rep. Argentina) and some consideration about the PEG Model. *Arch. Hydrobiol.* **127**, 167–184.
- Diéguez M. C. & Balseiro E. G. (1997) Colony size in *Conochilus hippocrepis*: defensive adaptation to predator stage sizes. *Hydrobiologia* (in press).
- Diéguez M. C., Modenutti B. E. & Queimaliños C. P. (1997) Influence of food resources on body size of *Keratella cochlearis* (Gosse) in a small Andean lake. *Hydrobiologia* (in press).
- Foissner W. & Wölf S. (1994) Revision of the genus *Stentor* Oken (Protozoa, Ciliophora) and description of the *S. araucanus* nov. spec. from South American Lakes. *J. Plankton Res.* **16**, 255–289.
- Gaglioti P. V. (1993) Efectos del pastoreo en la comunidad de algas adheridas de un ambiente léntico andino. *XVI Reunión Argentina de Ecología*: 43.
- Lehman J. T. (1984) Grazing, nutrient release, and their impacts on the structure of phytoplankton communities. In: *Trophic Interactions within Aquatic Ecosystems* (eds D. G. Meyers & J. R. Strickler) pp. 49–72. American Assoc. Adv. Sci. Select. Symp. 85. Boulder.
- Linklater W. (1995) Breakdown and detritivore colonisation of leaves in three New Zealand streams. *Hydrobiologia* **306**, 241–250.
- Matveev V. & Balseiro E. G. (1990) Contrasting responses of two cladocerans to changes in the nutritional value of nanoplankton. *Freshwat. Biol.* **23**, 197–204.
- Modenutti B. E. (1988) Presencia de *Ophrydium naumanni* Pejler (Ciliophora, Peritricha) en lagos rionegrinos. *Neotropica* **36**, 99–103.
- Modenutti B. E. (1993) Summer population of *Hexarthra bulgarica* in a high altitude lake of South Andes. *Hydrobiologia* **259**, 33–37.
- Modenutti B. E. (1994) Spring-summer succession of planktonic rotifers in a South Andes lake. *Int. Rev. gesam. Hydrobiol.* **79**, 373–383.
- Modenutti B. E. (1997) Distribución de los Ciliados Planctónicos *Ophrydium naumanni* y *Stentor araucanus* en Lagos Oligotróficos Andinos. *Rev. Soc. Mex. Hist. Nat.* **47**, 79–83 (in Spanish with English abstract).
- Modenutti B. E., Balseiro E. G. & Cervellini P. (1993) Effect of selective feeding of *Galaxias maculatus* (Salmoniforme, Galaxiidae) on zooplankton of a South Andes lake. *Aquat. Sci.* **55**, 65–75.
- Modenutti B. E., Balseiro E. G. & Moeller R. (1998) Vertical distribution and resistance to ultraviolet radiation of a planktonic ciliate, *Stentor araucanus*. *Verh. int. Verein. Limnol.* **26**, 1636–1640.
- Morris D., Zagarese H., Williamson C. *et al.* (1995) The

- attenuation of UV radiation in lakes and the role of dissolved organic carbon. *Limnol. Oceanogr.* **40**, 1381–1391.
- Pedrozo F. L., Chillrud S., Temporetti P. & Díaz M. M. (1993) Chemical composition and nutrient limitation in rivers and lakes of northern Patagonian Andes (39°5′–42°S; 71°W) (Rep. Argentina). *Verh. Internat. Verein. Limnol.* **25**, 207–214.
- Peters R. H. (1975) Phosphorus regeneration by natural populations of limnetic zooplankton. *Verh. int. Verein. Limnol.* **19**, 273–279.
- Petersen R. C. & Cummins K. W. (1974) Leaf processing in a woodland stream. *Freshwat. Biol.* **4**, 343–368.
- Queimaliños C. P. (1993) Efectos del zooplancton sobre la sucesión del fitoplancton en un ambiente lacustre andino. Tesis Doctoral, FCEyN, UBA (in Spanish).
- Queimaliños C. P. (1997) Some physical and biological factors affecting a spring-summer phytoplankton dynamics in a shallow, temperate lake of south Andes (Argentina). *Internat. Revue ges. Hydrobiol.* **82**, 147–160.
- Queimaliños C. P. & Modenutti B. E. (1993) Experimental analysis of the rotifer-cladoceran effect on phytoplankton. *Verh. int. Verein. Limnol.* **25**, 943–946.
- Queimaliños C. P., Modenutti B. E. & Balseiro E. G. (1998) Phytoplankton responses to experimental enhancement of grazing pressure and nutrient recycling in a small Andean lake. *Freshwat. Biol.* **40**, 41–49.
- Quirós R. (1998) Fish effects on trophic relationship in the pelagic zone of lakes. *Hydrobiologia* **361**, 101–111.
- Rowe J. M., Meegan S. K., Engstrom E. S., Perry S. A. & Perry W. B. (1996) Comparison of leaf processing rates under different temperature regimes in three headwater streams. *Freshwat. Biol.* **36**, 277–288.
- Sedell J. R., Triska F. J., Hall J. D., Anderson N. H. & Lyford J. H. (1974) Sources and fates of organic inputs in coniferous forest streams. *Conif. Forest Biom.* **5**, 57–69.
- Shapiro J. (1980) The importance of trophic-level interactions to the abundance and species composition of algae in lakes. In: *Hypertrophic Ecosystems* (eds J. Barica & L. R. Moore) pp. 105–116. Junk Publisher, The Hague.
- Short R. A., Canton S. P. & Ward J. V. (1980) Detrital processing and associated macroinvertebrates in Colorado mountain stream. *Ecology* **61**, 727–732.
- Thomasson K. (1963) Araucanian Lakes. *Acta Phytogeogr. Suec.* **47**, 1–139.
- Valverde A. C. & Albariño R. J. (1997) Descripción de los estados inmaduros de *Myotrichia murina* Schmid y *Parasericostoma cristatum* Flint (Trichoptera: Sericostomatidae). *Rev. Soc. Entomol. Argent.* **57** (in press).
- Vega A. P. M. (1995) Morphology and defensive structures in the predator-prey interaction: An experimental study of *Parabroteas sarsi* (Copepoda, Calanoida) with different cladoceran prey. *Hydrobiologia* **299**, 139–145.